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MODELING SEX-SPECIFIC SEASONAL HABITAT SELECTION FOR ELK (CERVUS ELAPHUS) IN CENTRAL WASHINGTON

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MODELING SEX-SPECIFIC SEASONAL HABITAT SELECTION FOR ELK (CERVUS ELAPHUS) IN CENTRAL WASHINGTON

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by

Lewis Meyers

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Graduate Studies

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ABSTRACT

MODELING SEX-SPECIFIC SEASONAL HABITAT SELECTION FOR ELK (CERVUS ELAPHUS) IN CENTRAL WASHINGTON

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Abstract: Elk (*Cervus elaphus*) are generalist herbivores, exploiting a variety of environments. I studied habitat selection and sexual segregation of the Colockum elk herd in central Washington. I used a resource selection probability function (RSPF) to evaluate habitat use by males and females during summer and winter seasons. I assisted Washington State Department of Fish and Wildlife (WDFW) in capturing and placing GPS collars on males, and used an existing GPS dataset from females to investigate the extent to which sexual segregation was occurring in the Colockum herd. During summer, males selected steep slopes on north, west and south aspects at high elevations near water sources and roads. They selected vegetation with high photosynthetic activity modeled using a normalized difference vegetation index (NDVI) in forested and semi desert land cover types. During summer, females selected gentler slopes than males, and with primarily southwest aspects, also at high elevations near water sources and roads in forest and semi desert cover types. Females differed from males in referring to areas where vegetation had lower photosynthetic activity and shrub land cover. During winter, males selected moderate slopes with south and northeast aspects at moderate elevations near roads in forested, semi desert and shrub land cover types. During winter, females also selected moderate slopes, but with a broader variety of aspects than males did (south, west, and north). Like males, females selected

shrub land, semi desert, and forest cover types at moderate distances from water. I concluded that predation risk, scramble competition and forage selection hypotheses are capable of explaining the differential use of habitats between males and females, depending on the season.

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CHAPTER I

GENERAL INTRODUCTION

Elk (*Cervus elaphus*) inhabit shrub land, grassland, and a variety of forest habitats across North America (Lyon and Christensen 2002). In the 1800s elk occupied most of the United States, but were eventually extirpated from much of the eastern and southwestern portions of the country (O'Gara and Dundas 2002). During the last century, elk populations have increased; in 1999 it was estimated that 780,000 elk existed in the U.S. largely due to translocations and natural range expansions (Peek 2003). Some elk populations occupy the same range throughout the year (non-migratory), while others migrate annually in the spring and fall to separate summer and winter ranges (migratory; Peek 2003). The migration period can vary in length from several days up to 2 months and likely reflects availability of edible forage which may be strongly influenced by snow accumulation and plant phenology (Irwin 2002). As ecological generalists, elk use diverse habitats across geographic regions, seasons, and latitudes (Bonenfant et al. 2004).

Habitat selection by female elk has been studied more extensively (McCorquodale 2003, Unsworth et al.1998) because female survival and reproduction drives elk population dynamics. The differential use of space by males and females, or social separation can be called sexual segregation (Bowyer 2004), though some believe that a widely accepted definition of the term is lacking (MacFarlane and Coulson 2005). Sexual segregation in ungulates is common outside of breeding seasons, but evolutionary cause(s) for segregation are not fully understood (Ruckstuhl 2007, Ruckstuhl and Neuhaus 2002, Bowyer 2004). By focusing research exclusively on either males or females there is the possibility that management strategies, particularly habitat conservation, could be tailored too much to one sex or the other. Understanding behavior of both

sexes relative to seasonal habitat selection would provide more useful information to wildlife managers.

CHAPTER II

LITERATURE REVIEW

Substantial research has been conducted on elk, including social behavior (Altmann 1951), population ecology (Coughenour and Singer 1996), and factors influencing habitat use (Lyon 1979). Conservation of suitable habitat for elk and other wildlife is an ongoing management challenge. By better understanding elk habitat use we can promote management objectives to keep elk productive, well-distributed, and common. Elk habitat selection and usage patterns vary across geographic regions and seasons (Bonenfant et al. 2004). However, elk have often been shown to select habitat based on slope, aspect, elevation, vegetation cover type, distance to roads, and water sources (Sawyer et al. 2007, McCorquodale 2003, Profitt et al. 2012, Severson and Medina 1983).

Elk tend to avoid open roads (Montgomery et al. 2013, Sawyer et al. 2007), but may also adjust to areas with high road densities when adequate vegetative and topographical cover exist (Lyon 1979). Migratory elk tend to prefer higher elevations during summer and lower elevations during winter (Sawyer et al. 2007, McCorquodale 2003). In other cases, however, older males have been observed wintering in deep snow areas at higher elevations (Unsworth et al. 1998). Elk generally prefer gentle to moderate slopes with grades less than 40% and rarely use topography with slopes above a 60% grade (Edge et al. 1987, Mackie 1970). In winter, elk spend their time on upper south and west-facing aspects, likely because wind and increased sun exposure melt the snow pack quicker there, making forage more available (Dalke et al. 1965, Severson and Medina 1983). In summer, northern aspects at higher elevations with substantial tree canopy cover are often selected, likely because these environments provide cooler habitats and delayed forage senescence (Skovlin et al. 2002). Habitat edges are important to elk because

they provide forage (openings) and security areas (cover) in close proximity to each other (Thomas et al. 1979, 1988). Forest cover and diverse topography provide areas of refuge for elk from hunting, logging and other disturbances (Mao et al. 2005). Elk can also be successful in non-forested environments where sparse tree cover exists (Eberhardt et al. 1996). Because elk are dimorphic (males are larger than females), habitat use may differ between the sexes.

Sexual segregation is common among wild ungulates and reflects sex-specific strategies for reproductive success and different constraints on fitness. Evolutionary cause(s) for segregation are not fully understood (Ruckstuhl 2007, Ruckstuhl and Neuhaus 2002, Bowyer 2004), but a well-developed theoretical discussion of sexual segregation is embodied in published literature on this topic. Conradt (2005) postulated that ungulates segregate by gender as adults at 3 scales: social, spatial, and habitat. Conradt (2005) cautioned that spatial segregation should be treated as an auxiliary concept because both habitat and social segregation can lead to spatial segregation. There are several hypotheses that have been presented explaining why habitat segregation occurs. Hypotheses promulgated to explain habitat segregation in ungulates typically invoke differences in body sizes between the smaller females and larger males, combined with sex-specific strategies for lifetime reproductive success. Dimorphism leads to differences in digestive capabilities, reproductive strategies and vulnerability to predation (Ruckstuhl 2007).

There are 3 hypotheses most commonly associated with habitat segregation. The predation-risk hypothesis states that males will seek higher quality forage even if it presents a greater danger from predators (e.g., because these settings are in openings), whereas females will select for habitats with more cover to protect their offspring even though forage quality might be lower (Main et al. 1996). Elk are a polygynous species where one male mates with multiple

females, provided he can out compete other males. Clutton-Brock et al. (1980) found that fighting success for red deer was strongly associated with body and antler size. Thus, it is important for males to be healthy when the reproduction period (rut) comes around so they have the best chance at mating with females. The possibility for males being able to pass on more genetic material per year than females would explain why males would accept risk in order to access higher quality forage. Given that a female can only raise one offspring per year it is more advantageous for her to ensure the survival of her calf by using areas with better cover. This hypothesis is also supported by research on Nubian ibex (*Capra ibex nubian*, Kohlmann et al. 1996). The authors found that females whose offspring were confined to safe ledges were able to leave them behind and therefore fed more often than females that kept their young with them in habitats that presented higher vulnerability to predation (Kohlmann et al. 1996).

The forage selection hypothesis explains that females select high quality forage due to small body size and lactation requirements, whereas males select areas with high forage biomass (Beier 1987; Barboza and Bowyer 2000). This has been illustrated well in white tailed deer (*Odocoileus virginianus*; Beier 1987). Due to sexual dimorphism, males have a lower mass specific metabolic rate given their gut capacity when compared to females (Beier 1987). Males can thus exploit lower quality, but more abundant forage than females. Beier (1987) found that female white tailed deer had higher levels of fecal nitrogen than males, which supported the conclusion that females chose higher quality forage than males did.

The scramble competition hypothesis reasons that the sexes separate because one will out-compete the other in preferred feeding sites (Clutton-Brock et al. 1987). This is one of the least accepted hypotheses explaining sexual segregation (Ruckstuhl 2007). Female elk commonly form large groups when using open areas (Proffitt et al. 2012) and if an area is small

enough then this could lead to competitive exclusion, but that is unlikely. Clutton-Brock et al. (1987) removed female red deer (*Cervus elaphus*) from known feeding sites but males did not move back into those areas. It is likely that because of the greater dietary range of larger males, ungulates would rarely compete for forage thus limiting the potential of explaining this in ungulates (Pérez-Barbería and Gordon 2000). Segregation by sex and age classes is a complex phenomenon that cannot be explained by one hypothesis in red deer (Alves et al. 2013). It is also possible that, due to temporal restrictions, habitat preferences between the sexes may change from winter to summer seasons (Ruckstuhl and Nehaus 2000, 2002).

CHAPTER III

CONCLUSION

Given that the majority of research has focused on female elk (McCorquodale 2003), habitat needs of males are not understood to the same degree. To address this issue I used data collected from global positioning satellite (GPS) collars to track elk movements of both male and female elk in the Colockum herd in central Washington. This allowed me to model habitat selection in regards to summer and winter seasons using resource selection probability functions and geographic information system (GIS) data. By understanding the extent of habitat segregation between the sexes in summer and winter, I sought to confirm if habitat selection differed between males and females each season. I considered current hypotheses explaining habitat segregation in ungulates as supported by my data. This information potentially advances knowledge of the differences in habitat use and allows managers to make better informed decisions. In the future, this information could be used to help guide management strategies for elk herds in similar geographic and ecological conditions.

Chapter IV

MODELING SEX-SPECIFIC SEASONAL HABITAT SELECTION FOR ELK (*CERVUS ELAPHUS*) IN CENTRAL WASHINGTON

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broader variety of aspects than males did (south, west, and north). Like males, females selected shrub land, semi desert, and forest cover types at moderate distances from water. I concluded that predation risk, scramble competition and forage selection hypotheses are capable of explaining the differential use of habitats between males and females, depending on the season.

Key Words. Elk, *Cervus elaphus*, Colockum herd, Washington, Washington Department of Fish and Wildlife, Habitat segregation, Habitat

Introduction

Elk (*Cervus elaphus*) are generalist herbivores, inhabiting a variety of shrub land, grassland, and diverse forest habitats across North America (Lyon and Christensen 2002). The Colockum elk herd, one of many elk herds in the state, is located in central Washington, north of Ellensburg (Figure 1). Some elk populations occupy the same areas seasonally throughout the year (non-migratory), whereas others, such as the Colockum herd, migrate annually in the spring and fall to separate summer and winter ranges (migratory; Peek 2003). The migration period can vary in length from several days up to two months and is associated with seasonal dynamics of forage availability and phenology and with snow accumulation (Irwin 2002).

Elk habitat use and the factors influencing it, vary across geographic regions, seasons, and latitudes (Bonenfant et al. 2004). Slope, aspect, elevation and distance from roads are frequently important factors influencing elk habitat use (Sawyer et al. 2007). Elk may avoid open roads (Montgomery et al. 2013, Sawyer et al. 2007), but may also adjust to areas with high road densities when adequate vegetative and topographical cover exist (Lyon 1979). Elevation is important to migrating elk herds, as they tend to prefer higher elevations during summer and lower elevations during winter (Sawyer et al. 2007, McCorquodale 2003), although adult male elk have been observed wintering in deep snow areas at higher elevations (Unsworth et al. 1998). Elk prefer gentle to moderate slopes ($\leq 40\%$) and rarely use slopes $\geq 60\%$ (Edge et al. 1987,

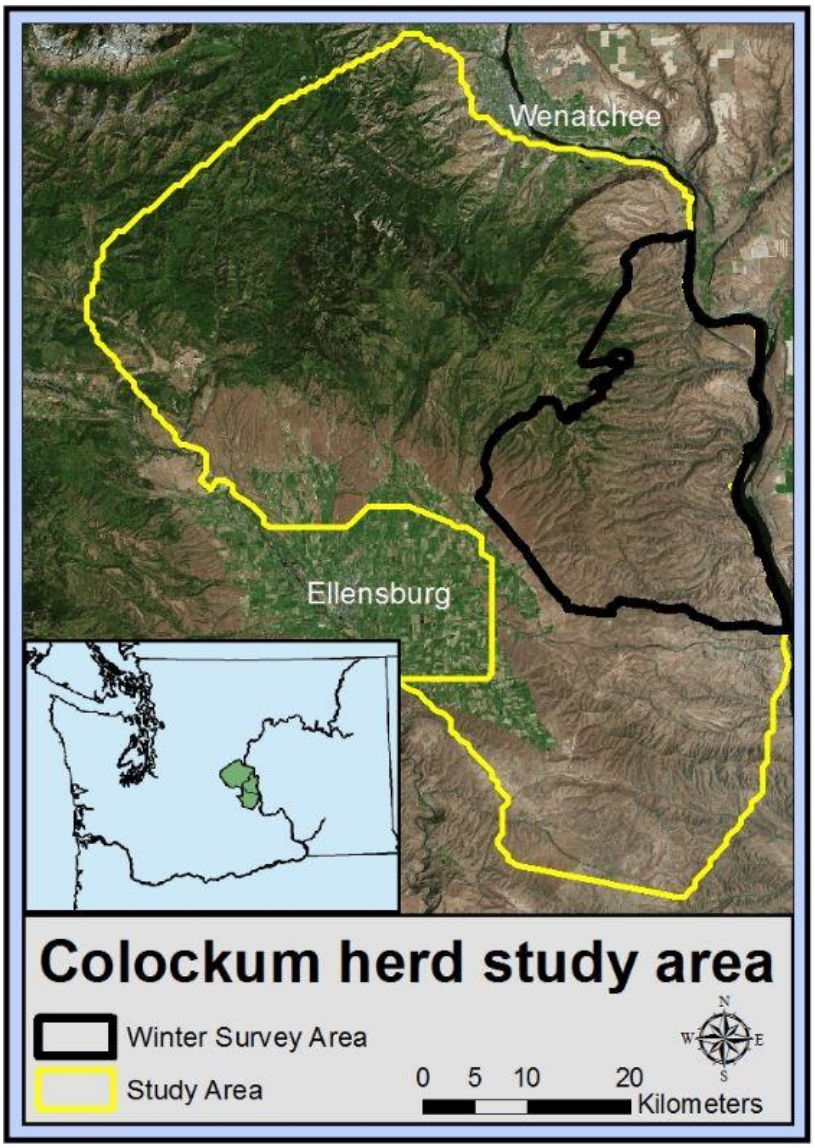

Figure 1 The Colockum herd study area (yellow) defined by minimum convex polygon around male and female elk GPS locations and natural and manmade barriers during the summer and winter seasons. WDFW's winter survey area is shown in black, annual elk counts are conducted here.

Mackie 1970). Sawyer et al. (2007) found no difference in slope preference between winter and summer ranges for an elk herd in a high elevation cold desert in southwestern Wyoming. In winter, elk often use upper south and west-facing aspects, likely because wind and increased solar radiation melt snow packs quicker, making forage more available (Dalke et al. 1965, Severson and Medina 1983). In summer, northern aspects at higher elevations with canopy cover are often selected, because they usually provide cooler habitats and more delayed forage

senescence (Skovlin et al. 2002). Land cover is important for elk habitat use because it assists them in avoiding predators, especially in hunted elk herds where edge habitat is preferred (Thomas et al. 1979, 1988). Forests, vegetation and topography provide areas of refuge for elk from human hunting and other disturbances (Mao et al. 2005). Elk can also occupy non-forested environments where sparse tree cover exists (Sawyer et al. 2007; Eberhardt et al. 1996).

While it is important to understand overall habitat use in elk, it is also important to know that males and females can differ in patterns of habitat use. Most elk habitat use studies have focused on females (Unsworth et al.1998). Their behavior has been studied more than males because fertility and female survival drives population dynamics. However, the phenomenon of sexual segregation has clearly highlighted how male and female ungulates can use their respective ranges differently, though evolutionary cause(s) for segregation are not fully understood (Ruckstuhl 2007, Ruckstuhl and Neuhaus 2002, Bowyer 2004). Sexual segregation is a hotly debated topic (MacFarlane and Coulson 2005) and no unifying theory has emerged. Recently Alves et al. (2013) suggested that segregation by sex and age classes is a complex phenomenon that cannot be explained by one hypothesis. Conradt (2005) noted that species segregate in 3 contexts; social, spatial, and/or habitat. Conradt (2005) cautioned that spatial segregation should be treated as an auxiliary concept because both habitat and social segregation can lead to spatial segregation. Ruckstuhl (2007) suggested that to understand the evolutionary origins of sexual segregation, research should shift studies away from species that sexually segregate and instead focus on species that should sexually segregate, but do not. Ruckstuhl (2007) also believed that it was best to analyze habitat and social segregation separately. I focused my research on habitat segregation.

The 3 leading hypotheses on habitat segregation are the predation-risk, forage selection, and scramble competition hypotheses (Ruckstuhl 2007). The predation-risk hypothesis posits that males will risk accessing higher quality forage even if it presents a greater danger from predators, whereas females will select for habitats with more security to protect their offspring even if the forage quality might be lower (Main et al. 1996). For my data this hypothesis might yield a pattern of strong selection for high NDVI values for males relative to females. I would also expect to see females avoiding open habitats and roads and selecting more forest and shrub covered areas.

The forage selection hypothesis suggests that females should select high quality forage due to bioenergetics of smaller body size and lactation requirements, whereas males should select for areas with high forage biomass (Beier 1987; Barboza and Bowyer 2000). If true, females should select for areas with higher NDVI reflectance. Areas near water should be highly sought after by females during mid to late summer because of higher forage quality senescence of vegetation in open habitats. In winter I would expect females to select lower elevations in semi desert and shrub land cover types to avoid high snow pack and to access forage more readily (Trottier et al. 1983).

The scramble competition hypothesis posits that the sexes separate because one out-competes the other in preferred feeding sites (Clutton-Brock et al. 1987). This hypothesis would be the most difficult to support given that it requires a control and exclusion area to show that one sex is actually outcompeting the other for feeding sites. For example, Clutton-Brock et al. (1987) experimentally removed females from preferred feeding sites however; males did not move in to re-occupy the area. It could be that the greater dietary range of larger male ungulates would cause them to rarely compete for forage with females thus limiting the potential of

explaining this hypothesis in ungulates (Pérez-Barbería and Gordon 2000). If this hypothesis were relevant, I would expect to see a difference in use between males and females in topographic features (slope, elevation and aspect). This could be consistent with avoidance of one sex from the other.

Knowing what makes a habitat suitable for each sex and why is a challenge for managers. By gaining a more thorough understanding of habitat affinities, wildlife managers can promote management objectives to keep elk widely distributed and common. With this in mind, I set out to explore sex-specific habitat selection and potential sexual segregation in the Colockum elk herd in central Washington. I investigated habitat use by male and female elk across summer and winter ranges. My objectives were to: 1) use adult male and female GPS-locations to model habitat selection patterns to determine if male and female elk were selecting different habitat characteristics. 2) Map areas of high and low probability of use by season and sex based on the outcome of my selection modeling. 3) Examine my results for evidence supporting the 3 most commonly supported habitat segregation hypotheses.

Study Area

For the purposes of my study I created a minimum convex polygon (MCP) around the collective GPS locations obtained from research on male and female Colockum elk since 2008 and added a 250-m buffer around the MCP. I constrained the subsequent study area by using logical natural and artificial boundaries (Figure 1). These boundaries were the Yakima River to the northwest and the Columbia River to the east. Artificial boundaries included Interstate Highway 82 on the southwest edge and U.S. Highway 2 on the northern edge. These artificial and natural boundaries were used because radiomarked elk never crossed them. I also excluded the urban areas of Wenatchee and Ellensburg because radiomarked elk also did not use those

areas. The 3,060-km^2 study area encompassed a mosaic of public and private lands. Notable features of this landscape included the Wild Horse Wind Farm, Mission Ridge Ski & Board Resort and rural and agricultural areas surrounding the city of Ellensburg. Public lands were managed by the Washington Department of Fish and Wildlife (WDFW), Washington Department of Natural Resources (WDNR), U.S. Bureau of Land Management (BLM) and the U.S. Forest Service (USFS) and included WDFW's Quilomene, Whiskey Dick, and Colockum Wildlife Area Units, along with parts of the WDNR Teanaway Community Forest and the USFS Okanogan-Wenatchee National Forest (WDFW 2006). The southernmost end of the study area extends into the U.S. Army's Yakima Training Center which is used for military training.

Geographically, the study area was in the Northern Washington Cascades and Columbia Basin Provinces (Franklin and Dyrness 1973). Elevations ranged from 2,100-m to 170-m (CWU 2013). In the summer, climate was typified by hot dry conditions (June – September), with temperatures in the lower valleys reaching highs around 38ºC and lows down to 16ºC. During winter (December – March) typical high temperatures ranged from -1 – 5ºC, while minimums ranged from -12 – -6ºC. Summers were dry, but winter precipitation was relatively common. On the east end of the study area annual precipitation was typically < 25 cm; on the west end precipitation ≥ 254 cm was possible at the highest elevations. Snowfall of 25 – 100 cm was typical in low elevations and could be up to 178 cm at the highest elevations. At lower elevations, snow seldom remained on the ground for longer than six weeks (WDFW 2006).

The eastern and southern most parts of the study area were dominated by shrub-steppe communities (Daubenmire 1970). The western side of the study area consisted of a diverse assortment of high and low elevation forests. Overstories were variously dominated by Ponderosa pine (*Pinus poderosa*), grand fir (*Abies grandis*), Engelmann spruce (*Picea*

engelmanni), western larch (*Larix occidentalis*), and Douglas fir (*Pseudotsuga menziesii*). Understory components included Oregon grape (*Berberis nervosa),* Spirea *(Spirea betufolia),* ocean spray *(Holodiscus discolor),* sagebrush, antelope bitterbrush *(Purshia tridentata),* cinquefoil (*Potentilla spp*), heartleaf arnica (*Arnica cordifolia*), arrowleaf balsamroot (*Balsamorhiza sagittata*), lupine (*Lupinus spp*), western yarrow (*Achillea millefolium*), vetch (*Astragalus spp*), and snowbrush *(Ceanothus velutinus).* Important shrubs included serviceberry (Amelanchior spp), currant *(Ribes spp),* barberry *(Berberis spp),* huckleberry (*Vaccinium spp*), mountain boxwood *(Pachistima myrsinites),* and mountain snowberry *(Symphoricarpos albus)* (Franklin and Dyrness 1973). Other wild ungulates in the area included mule deer (*Odocoileus hemionus*), mountain goats (*Oreamnos americanus*), and bighorn sheep (*Ovis canadensis california*). Domestic ungulates such as cattle, horses and sheep also occur in areas of the Colockum herd's core range and vary from season to season (WDFW 2006).

Methods

Capture and Monitoring

Female elk data were derived from a previous study of the Colockum herd by WDFW (2008 – 2012). To generate space use data for male elk, WDFW biologists darted them from a helicopter with a mixture of carfentanil citrate and xylazine hydrochloride. Captured males were blind-folded during handling to reduce stress, ear tagged, and fitted with GPS-collars (LifeCycle Collar, Lotek Wireless Inc., Newmarket, Ontario, Canada). Immobilizations were reversed using naltrexone hydrochloride and tolazoline hydrochloride. All immobilization and handling of study animals complied with protocols established by a professional Wildlife Veterinarian. Collars deployed on males were set to obtain GPS fixes every 13 hours. This interval offset daily fix times each day to obtain locations at all times of day. The female elk data set derived from WDFW's earlier study had been generated with 3 hour fix intervals due to different objectives. Collars were equipped with a mortality sensor that would send out an email and change the VHF pulse when the animal remained motionless for longer than 8 hours. Between September 2013 and September 2016, WDFW fitted a total of 54 adult male elk with GPS-collars. During the last field capture, 12 new collars (Survey Globalstar, Vectronic Aerospace GmbH, Berlin, Germany) were used instead of the original Lotek collars. To locate failed GPS transponders, fixed wing aircraft flights were periodically used to search for VHF tracking signals. Fix success bias for male elk was not an issue because of a high success rate of the collars (89%) and I did not differentially correct GPS locations because 91% of the locations were 3-dimensional. Fix success bias for female elk was also not an issue because of a 90% success rate and GPS locations were not corrected because 89% of the locations were 3-dimensional.

Geographic Information System (GIS)

I searched United States Geological Survey (USGS), Central Washington University (CWU) and WDFW data sources for available GIS data in my study area. I found data that allowed me to analyze 8 habitat variables potentially useful for modeling elk habitat selection in the Colockum herd. GIS layers reflected data for elevation, slope, aspect, land cover types, roads, hydrology (i.e. streams & rivers), wetlands, and availability of photosynthetically active vegetation (using a normalized difference vegetation index: NDVI). I used ArcGIS (version 10.3) software with the ArcMap extension to derive slope (%) and aspect class data (north, northeast, east, southeast, south, southwest, west, and northwest) from a 30 x 30-m digital elevation model (CWU 2013). A digitized road map was provided by WDFW (unpublished data) that included all paved, gravel, and dirt roads within the study area. Roads were classified into 4 categories: paved, maintained gravel, unmaintained gravel, and closed roads. For the summer analyses, all road types were included, even closed roads because they received consistent foot traffic (personal observation). For winter analyses I excluded closed and unmaintained gravel roads because snowfall made these impassable for vehicles. All roads under winter closures were also excluded. A 30 x 30-m land cover map was obtained from the USGS Land Cover Institute (2011) with 6 cover types: forest, human use (urban and city limits), recently disturbed (recreation areas), semi-desert (areas devoid of sagebrush, mainly consisting of various grass species), shrub land (areas containing sagebrush) and other. The national land cover data set had also been used to classify land cover types in a Montana elk study in Wall Creek (Proffitt et al. 2012). I obtained wetland (2011) and stream (2011) vector GIS data from the Washington State Department of Ecology (2014) and used these data to create a raster grid representing distance in order to calculate their proximity to sampling units. NDVI data were captured from a 30 x 30-m

resolution Landsat 7 (satellite) raster image (USGS 2010 - 2015) for each summer (2011-12 & 2014-15) and winter (2010-12 & 2013-15). I only selected scenes that had less than 10% cloud cover. For summer, I searched for best available images in July and for winter I searched images taken in January as these times occurred in the middle of my sampling windows. I converted the raster image to NDVI values using ERDAS IMAGINE 2015 software and the NDVI equation (NIR-RED)/(NIR+RED), where NIR = near infrared spectral band raster image and RED = red spectral band raster image (Carlson and Ripley 1997). I censored closed canopy forests identified by the USGS land cover map (2011) because the forest canopy was the reflecting layer, not the understory where elk forage was located. The resulting NDVI values reflected the availability of photosynthetically active ground-level vegetation in the study area. NDVI has been used in other elk studies to model forage availability for elk (Cleveland et al. 2012, Middleton et al. 2013).

General Linear Model (GLM)

I used the methods outlined by Sawyer et al. (2006, 2007) to separately model habitat use of adult male and female elk in my study area for winter and summer seasons. This process involved 4 steps. The first step required creating a grid of circular sampling units within the study area using GIS. The second step required counting GPS locations for each individual elk that fell within the sampling units; this count served as an estimate of relative use for an individual elk within a season. Relative use for each elk was then used as a continuous response variable in a multiple regression analysis using habitat predictor variables to explain frequency of use across sampling units. The third step involved using average coefficients obtained from individual elk to create a population-level model for each sex during each season. Lastly, I mapped the predicted habitat use across my study area based on my population-level models.

I defined winter as November 15th to March 15th and summer as May 15th through September 15th. This allowed me to evaluate seasonal habitat selection apart from migration periods. I treated individual, GPS-collared elk as the experimental unit rather than pooling GPS locations from all elk, allowing me to avoid pseudoreplication (Sawyer et al. 2006, 2007) and to prevent any one elk from influencing the outcome of the model more heavily than others simply because it had more GPS locations (Otis and White 1999, Ericson et al. 2001, Millspaugh et al. 2006). No more than 10% of sample group sizes for males or females yielded fewer than 2 months worth of GPS fixes per individual so I included all study subjects in my population estimates. Due to data being collected for males from 2013 – 2015 and females from 2010 – 2012 during the winter season, I averaged counts for any individual that provided data in both winters. This gave me an average response for that individual. This was repeated for summer and was also done with males that overlapped into multiple years. This gave me one final summer and winter model for each individual. This was then averaged within season and sex to get the final coefficient for the population estimate. This allows for a general comparative analysis of each season.

Relative frequency of use was estimated by creating circular sampling units with a 500-m diameter (N =11,768) and systematically placing them in a non-overlapping grid across the defined study area. This was done by using the fishnet tool in ArcMap. The sampling unit size was chosen because it allowed me to detect small changes in each animal's movement but still allowed for multiple GPS locations to occur in each sampling unit (Sawyer et al. 2006, 2007). I collected measurements for all predictor variables in each sampling unit. Categorical variables (aspect and land cover) were given a value based on the mode of the pixel type that fell within that circle. Continuous variables (slope, elevation, NDVI as well as distance to roads, water, and

wetlands) were measured by the mean of the pixel values that fell within the circular sampling unit. I examined pairwise Pearson's correlation coefficients (Zar 1999, Zuur et al. 2009) to identify any with high multicollinearity. No variable pairs yielded correlation coefficients higher than 0.60; all predictor variables were thus retained in the analysis (Sawyer et al. 2006, 2007). I assessed linearity of the relationship between probability of use and all numerical predictor values using scatterplots (Zuur et al. 2009). All potential numerical predictor variables yielded linear relationships and were therefore included in the model.

During the study, slight variations in the number of recorded GPS locations occurred amongst each individual. To solve this issue I used the relative frequency of locations from each individual elk in each sampling unit to account for the probability of use by that elk. This was then used as my continuous response variable in a generalized linear model (GLM). I employed a negative binomial distribution using the lme4 package in R (version 3.2.1) because I had a large number of sampling units with 0 GPS locations and this distribution appropriately allowed for over dispersion (McCullagh and Nelder 1989, White and Bennetts 1996, Sawyer et al. 2007).

I developed a population-level model by first estimating coefficients for predictor variables for each individual elk for each season. I then averaged the coefficients to obtain a population level model for each season. This has also been referred to as a two-step method (Zurr et al. 2009). To estimate probability of use for each individual elk, I used an offset term in the model (total number of GPS fixes for an individual in that individuals model) which represented a function of the linear combination of my predictor variables, plus or minus an error term having a negative binomial distribution (McCullagh and Nelder 1989, White and Bennetts 1996, Sawyer et al. 2007). This style of modeling resource selection estimated the relative

probability of use as a function of the 8 predictor variables and, therefore, represented a resource selection probability function (RSPF; Manly et al. 2002)

I assumed GLM coefficients for each predictor variable for each animal were a random sample from a normal distribution (Seber 1984). The mean of that distribution represented the population-level effect of that predictor variable on probability of use. I estimated coefficients for the population-level model for both winter and summer periods for both males and females as individuals. I then averaged the coefficients by season and sex. I estimated the variance of each population level model coefficient by using the variation among GPS-collared elk (Sawyer et al. 2007).

This RSPF method has been used in other studies to model habitat selection of a given area. Examples include the modeling of habitat selection of Rocky Mountain elk (*Cervus elaphus*; Sawyer et al. 2007), Stellar's jay (*Cyanocitta stelleri*; Marzluff et al. 2004) and mule deer (*Odocoileus hemionus*; Sawyer et al. 2006). Making population-level inferences is not affected by auto- or spatial correlation because temporal autocorrelation among locations of an individual elk or spatial autocorrelation among habitat units does not bias model coefficients for the individual GPS-collared elk models (McCullagh and Nelder 1989, Neter et al. 1996).

I followed a forward-stepwise model-building procedure as was done by Sawyer et al. (2007) and Neter et al. (1996) to estimate population level models for male and female elk for a winter and summer season to get an estimate of average habitat use. This process required fitting the same model to each individual elk within each season and using the two step method to estimate population-level model coefficients. When an individual's coefficient for a predictor variable was insignificant I elected to keep it in the model to avoid bias towards overestimation of the absolute value of the coefficients. A *p*-value was used to determine significance ($\alpha \leq 0.05$)

of each predictor variable; non-significant predictors were eliminated from the predictive maps. To determine significance of categorical variables (aspect and land cover) I used a one-way analysis of variance (ANOVA) on coefficients for each category to confirm presence of variation. For aspect, the categorical predictor variable *east* was used as the reference and for land cover, *other* was used as the reference. If one or more of the aspect or land cover variables was significant ($\alpha > 0.05$) I chose to still include all the categories in the predictive map rather than express the effects of the nonsignificant categories to be equal (Sawyer et al. 2007).

Predictive Maps

For creating RSPF maps I used the population-level models created for each sex and season. I created probability maps that included effects for each significant predictor variable in each season for each sex. I used the raster calculator function in ArcMap with the function below to get a final map with the combined probability values of all significant predictor variables.

$$(i+(\beta_1 X_1)+ (\beta_2 X_2) + (\ldots)) = \text{Final Predictive Map Values}$$

Where X is the value of a given pixel on the predictor variable map, β represents the predictor variables coefficient and *i* is the intercept for a single season and sex. The resulting values were then split into quartiles. I reclassified values from the 75th and 100th percentile as being high probability of use, values between 50 and 74 being classed as medium-high, values between 25 and 49 medium-low and values <24 classed as low. Final probability maps used 30 x 30-m cells across the study area.

To validate predictive maps, I followed methods used by Sawyer et al. (2006, 2007) and used a sub-sample of GPS-collared males and females whose data had not been used to fit the

GLMs. I determined the percentage of GPS locations that fell within each class of predicted elk use. For the winter season test I used 12,537 GPS fixes taken from 19 individual adult females from the 2008 – 2009 winter. For the summer season I used 25,236 GPS fixes taken from 23 individual females taken from the summers of 2008 and 2009. For male elk model tests, I used a sample of 12 individuals taken from winter 2016, which consisted of 1,152 fixes and summer 2016, which consisted of 1,904 fixes. For maps to be considered successful lower classes could not have more fixes than the class above them (i.e., the number of fixes found in low areas can't be higher than the number of fixes in medium low areas and so on).

Results

Summer

Male RSPFs were based on 8,661 GPS fixes from 36 GPS-collared male elk over 2 summers (2014 and 2015). Most elk had positive coefficients that were significantly different from 0 for slope (63%), elevation (88%), NDVI (83%), westerly aspects (75%), north aspects (55%), and south aspects (77%). In the land cover category males had positive coefficients for forested (97%), and semi-desert (86%) cover types. Variables with negative coefficients different from 0 included distance to roads (66%), distance to water (66%), flat aspects (80%), and human use (58%) land cover. Distance to wetlands, northeast and southeast aspects, as well as recently disturbed and shrub land cover types were not useful predictors of male habitat selection ($\alpha > 0.05$) at the population level (Table 1).

Our final summer model for adult males included 7 of the 8 possible predictor variables (Table 1). Males tended to select for northern, western and southern aspects, on steep slopes (50% grade), at high elevations (1,200 – 1,450-m), close to roads (0 – 100-m) and water (0 – 100-m) in forested and semi desert land cover types.

For females I used 71 GPS-collared elk (92,483 locations), also averaged over 2 summers (2010 and 2011). Most elk had positive coefficients that were significantly different from 0 for elevation (97%) and southerly aspects (56%). Relative to land cover, females had positive coefficients for forested (83%), shrub land (88%), and semi-desert (81%) cover types. Variables with negative coefficients different from 0 included slope (85%), distance to roads (94%), distance to water (83%), NDVI (61%), flat (100%) as well as northerly aspects (70%), and human use (43%) land cover. Distance to wetlands, southeast, west and south aspects, as well as

recently disturbed land cover types were not useful predictors of female elk habitat selection ($\alpha > 0.05$) at the population level (Table 1).

The final adult female model included 7 of the 8 possible predictor variables (Table 1). Females tended to select for southwest aspects, on mild slopes (10 – 20% grade), at high elevations (1,450 – 1,700-m), close to roads (0 – 100-m) at moderate distances from water (300 – 400-m) in forest, shrub land and semi-desert land cover types.

Winter

For males, I used 35 GPS-collared elk (7,442 locations) averaged over the course of 2 winters (2013 – 2014 and 2014 – 2015). Most elk had positive coefficients that were significantly different from 0 for slope (94%), elevation (80%), southerly aspects (62%), and northeast aspects (62%). Males had positive coefficients for forested (57%), semi-desert (88%), and shrub land (62%) cover types. Variables with negative coefficients different from 0 included distance to roads (60%), flat aspects (77%), and human use (57%) and recently disturbed (100%) land cover. Distance to wetlands, distance to water, NDVI, and north, northwest, southeast, and west aspects were not useful predictors of male elk habitat selection ($\alpha > 0.05$) at the population level (Table 1).

The final adult male winter model included 5 of the 8 possible predictor variables (Table 1). Males tended to select for southern and northeast aspects, on steep slopes (40-50% grade), at moderate elevations (950 – 1,200-m), and distances from roads (400 – 500-m) in forest, semi-desert and shrub land cover types.

I developed RSPFs for females from 73 GPS-collared elk (81,482 locations) averaged over the course of 2 winters (2010 – 2011 and 2011 – 2012). Most elk had positive coefficients

Table 1 Results from general linear models for males and females, summer and winter season. Yellow highlight signifies a variable was included in the final predictive map. β = coefficient, *SE* = standard error, *F* = F-test, *DF* = degrees of freedom.

	Season											
	Male Summer			**Female Summer**			**Male Winter**			**Female Winter**		
Predictor Variables	**β**	***SE***	***P***	**β**	***SE***	***P***	**β**	***SE***	***P***	**β**	***SE***	***P***
Intercept	-35.809	2.836	<0.001	-19.766	1.493	<0.001	-22.834	4.281	<0.001	-23.967	1.719	<0.001
Slope(%)	1.069	0.368	0.006	-1.006	0.136	<0.001	1.754	0.206	<0.001	0.979	0.139	<0.001
Elevation(m)	2.858	0.542	<0.001	2.978	0.180	<0.001	1.154	0.221	<0.001	-0.154	0.281	0.584
Distance to wetlands(m)	0.148	0.268	0.583	-0.346	0.214	0.111	0.049	0.176	0.708	-0.333	0.068	<0.001
Distance to Roads(m)	-2.549	0.590	<0.001	-2.144	0.215	<0.001	-0.595	0.272	0.035	-0.357	0.077	<0.001
Distance to Water(m)	-1.101	0.276	<0.001	-0.951	0.117	<0.001	-0.539	0.308	0.089	-0.134	0.046	0.005
NDVI(reflectance)	5.873	1.276	<0.001	-1.759	0.727	0.018	-3.971	3.855	0.310	2.090	1.452	0.154
Aspect (reference: *east*)	***F*** = 7.588 ***DF*** = 7 ***P*** = <0.001			***F*** = 298.782 ***DF*** = 7 ***P*** = <0.001			***F*** = 7.719 ***DF*** = 7 ***P*** = <0.001			***F*** = 44.506 ***DF*** = 7 ***P*** = <0.001		
Flat	-6.692	1.600	-	-12.813	0.317	-	-8.459	1.207	-	-9.864	0.918	-
North	2.878	1.409	-	-1.368	0.444	-	1.603	1.578	-	1.521	0.576	-
Northeast	2.325	1.281	-	-0.383	0.127	-	2.852	1.312	-	-0.112	0.586	-
Northwest	3.043	1.483	-	-0.943	0.307	-	0.404	1.805	-	1.767	0.541	-
South	2.665	0.935	-	0.032	0.092	-	2.897	1.060	-	2.226	0.505	-
Southeast	-0.494	1.211	-	0.021	0.079	-	0.648	0.604	-	1.007	0.524	-
Southwest	3.536	1.064	-	0.236	0.113	-	3.810	1.219	-	2.163	0.529	-
West	4.076	1.185	-	-0.299	0.296	-	-0.142	1.874	-	1.631	0.596	-
Land Cover (reference: *other*)	***F*** = 13.812 ***DF*** = 5 ***P*** = <0.001			***F*** = 30.783 ***DF*** = 5 ***P*** = <0.001			***F*** = 22.788 ***DF*** = 5 ***P*** = <0.001			***F*** = 70.631 ***DF*** = 5 ***P*** = <0.001		
Human Use	-2.276	1.096	-	-3.788	0.802	-	-4.575	1.228	-	-6.132	0.898	-
Forest	10.543	1.250	-	9.527	0.937	-	4.155	1.593	-	3.593	1.158	-
Recently Disturbed	1.665	1.946	-	0.311	1.387	-	-5.881	1.272	-	-6.200	0.921	-
Semi Desert	8.803	1.268	-	7.708	0.874	-	10.126	1.226	-	9.792	0.852	-
Shrub land	1.227	1.597	-	6.294	0.903	-	5.830	1.812	-	9.919	0.927	-

that were significantly different from 0 for slope (82%), westerly aspects (68%), and north (61%) and south (87%) aspects. Females had positive coefficients for forested (63%), semi-desert (94%), and shrub land (90%) cover types. Variables with negative coefficients different from 0 included distance to wetlands (69%), distance to roads (60%), distance to water (56%), flat aspects (91%), and human use (61%) and recently disturbed (83%) land cover types. Elevation, NDVI, and southeast and northeast aspects were not useful predictors of female habitat selection ($\alpha > 0.05$) at the population level (Table 1).

The final adult female model included 6 of the 8 possible predictor variables (Table 1). Females selected for north, south and westerly aspects, on steep slopes (30 – 40% grade), at moderate distances from roads (1,000-m +), running water (100 – 300-m) and wetlands (1,500-m) in semi-desert, shrub land and forest cover types.

Sexual Segregation

During the summer I compared effect size of my coefficient means using 95% confidence intervals from my RSPFs (Figure 2). I compared predictor variables where both males and females had significant use of a variable ($\alpha < 0.05$) in my GLM. I also examined variables where one sex had significant use of a variable and the other did not. For categorical variables (aspect and land cover) I used ANOVA to see if elk significantly selected habitat variables. Female and male effect sizes differed in aspect, slope, and NDVI. Males preferred north facing aspects while females avoided them and males selected for southwest facing slopes more than females did, even though both had positive coefficients. Females were more likely to avoid steeper slopes than males, who selected for them and females selected for areas with lower NDVI values; males had positive coefficients for NDVI. For aspect, females only had positive coefficients for southwestern aspects and avoided all other aspects, whereas males had positive coefficients for

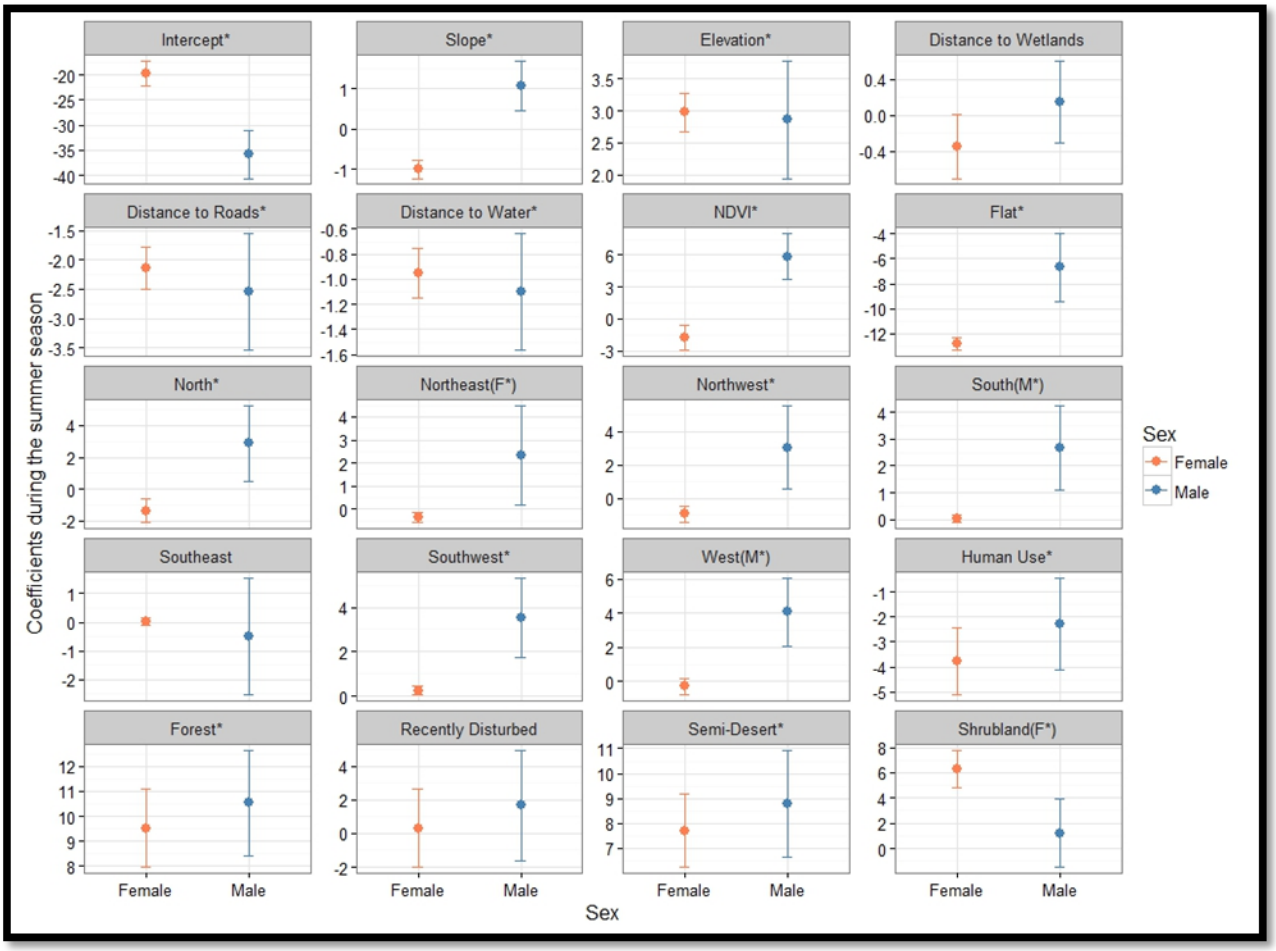

Figure 2 Coefficients for the summer season with 95% confidence intervals; females are orange and males are blue. F=females and M=males and an asterisk (*) denotes significant difference from 0 at the $\alpha = 0.05$ level. If an asterisk is present but no F or M is designated, then both sexes were significantly different from 0.

all aspect types with the exception of flat and east aspects. Male and female coefficients for land cover only differed in the shrub land cover type, where females had positive coefficients and males did not show significant selection.

In winter, effect sizes of coefficients between females and males differed only for slope where both sexes had positive coefficients, with females preferring slightly milder slopes than males did. Females selected for of distance to wetlands and distance to water variables, whereas males did not significantly use them. Males showed significant selection for high elevation while females did not. For aspect, females showed significantly higher use of north, northwest, and

west aspects while males did not and males showed significantly higher use of northeast aspects while females did not (Figure 3).

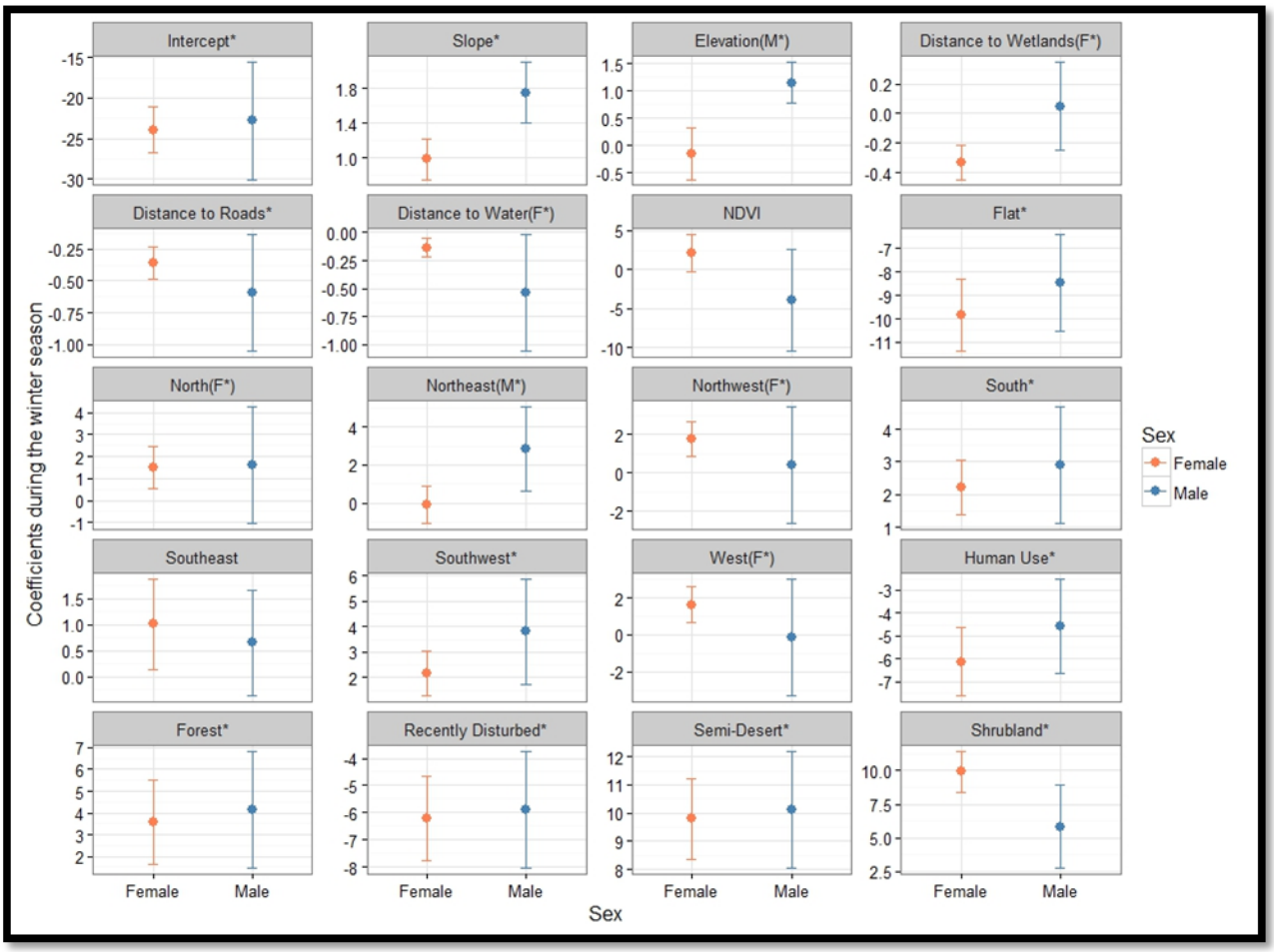

Figure 3 Coefficients for the winter season with 95% confidence intervals; females are orange and males are blue. F=females and M=males and an asterisk (*) denotes significant difference from 0 at the $\alpha = 0.05$ level. If an asterisk is present but no F or M is designated, then both sexes were significant from 0.

Predictive Map Validation

Summer

GPS fixes from 23 adult females and 12 adult males withheld from model building indicated that my models predicted summer habitat selection reasonably well (Tables 2, 3 and Figures 4, 5). Males and females had the most high and medium-high predicted use areas available to them in the northwestern portion of the study area. This is also where most GPS fixes were found. This area is characterized as higher elevation, higher forest cover (more shaded), higher road density and lower temperatures than the southeastern portion of the study area.

Table 2 Predictive map validation for females from summer 2009 sub-sample.

# Individual elk	23	
Predicted Use	**#Fixes**	**Percentage**
Low (0-24)	277	1
Medium-low (25-49)	840	3
Medium-high (50-74)	3,739	15
High (75-100)	20,376	81
Total	25,236	100

Table 3 Predictive map validation for males from summer 2016 sub-sample.

# Individual elk	12	
Predicted Use	**#Fixes**	**Percentage**
Low (0-24)	6	0
Medium-low (25-49)	138	**7**
Medium-high (50-74)	415	22
High (75-100)	1,345	71
Total	1,904	100

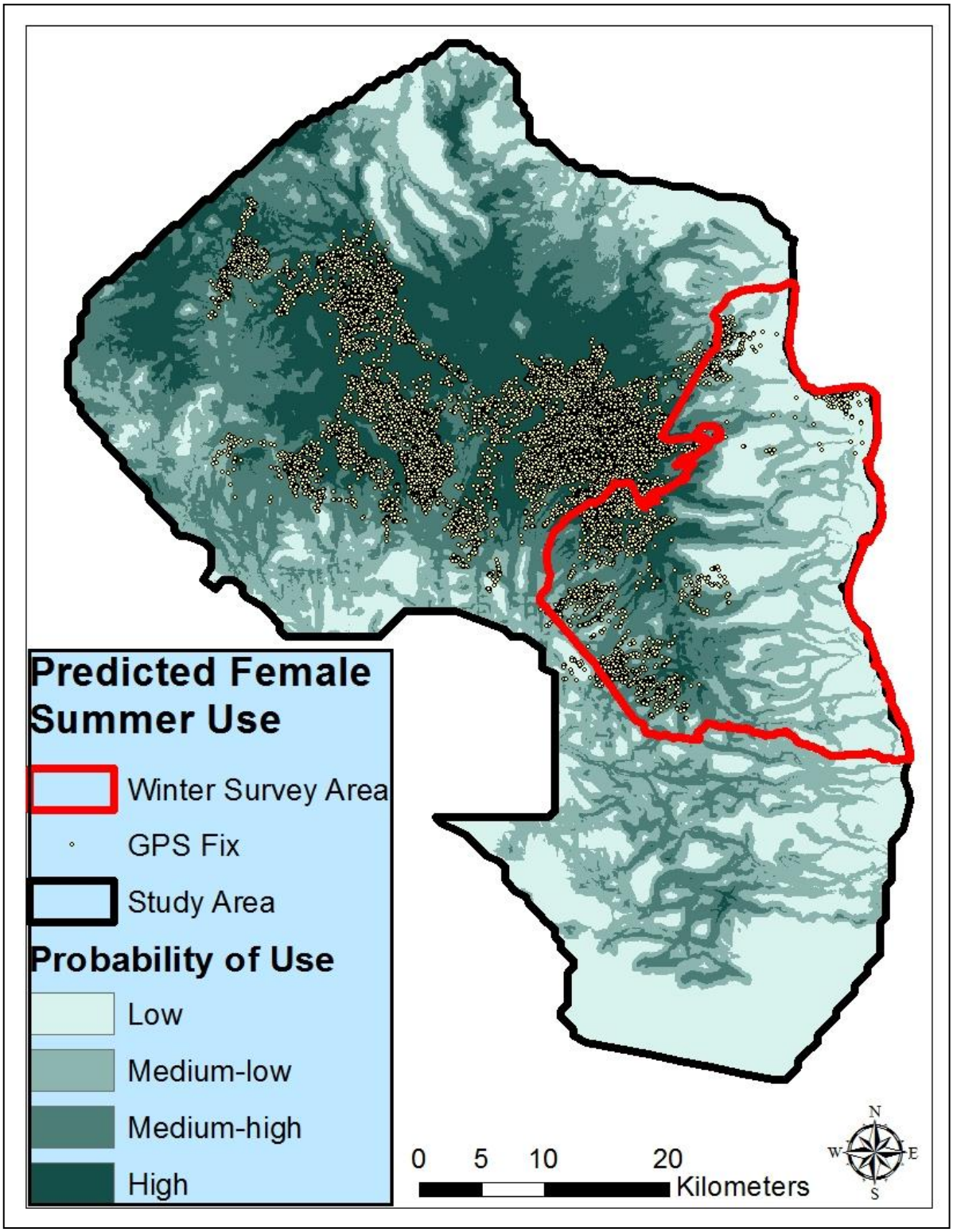

Figure 4 Predictive map showing areas of high and low use across the Colockum herds core range for adult females during the summer season.

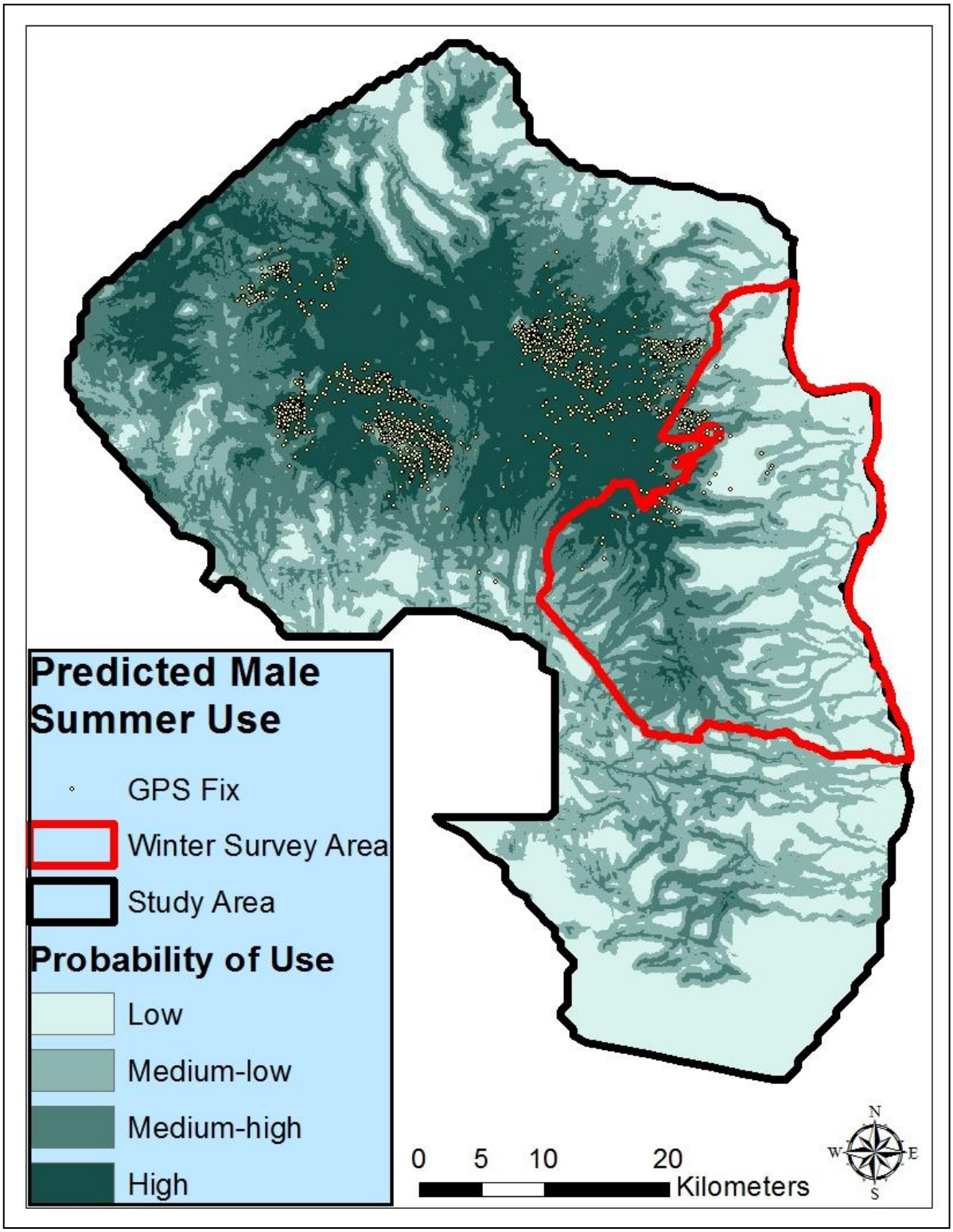

Figure 5 Predictive map showing areas of high and low use across the Colockum herds core range for adult males during the summer season.

Winter

GPS fixes from 19 adult females and 12 adult males withheld from model building indicated my models predicted winter habitat selection reasonably well (Tables 4, 5 and Figures 6, 7). Females had high and medium-high predicted areas of use available to them in most of the study area, but most fixes were found in the southern and eastern portions. This area is characterized by open habitat cover, warmer temperatures, lower road density, and less snow fall. Males had high and medium high predicted use areas over most of the study area in patches although most fixes were found in the east-central portion of the study area.

Table 4 Predictive map validation for females from winter 2008 – 2009 sub-sample.

# Individual elk	19	
Predicted Use	**#Fixes**	**Percentage**
Low (0-24)	1,755	14
Medium-low (25-49)	3,094	25
Medium-high (50-74)	3,218	26
High (75-100)	4,470	36
Total	12,537	100

Table 5 Predictive map validation for males from winter 2016 sub-sample.

# Individual elk	12	
Predicted Use	**#Fixes**	**Percentage**
Low (0-24)	39	3
Medium-low (25-49)	166	14
Medium-high (50-74)	308	27
High (75-100)	639	55
Total	1,152	100

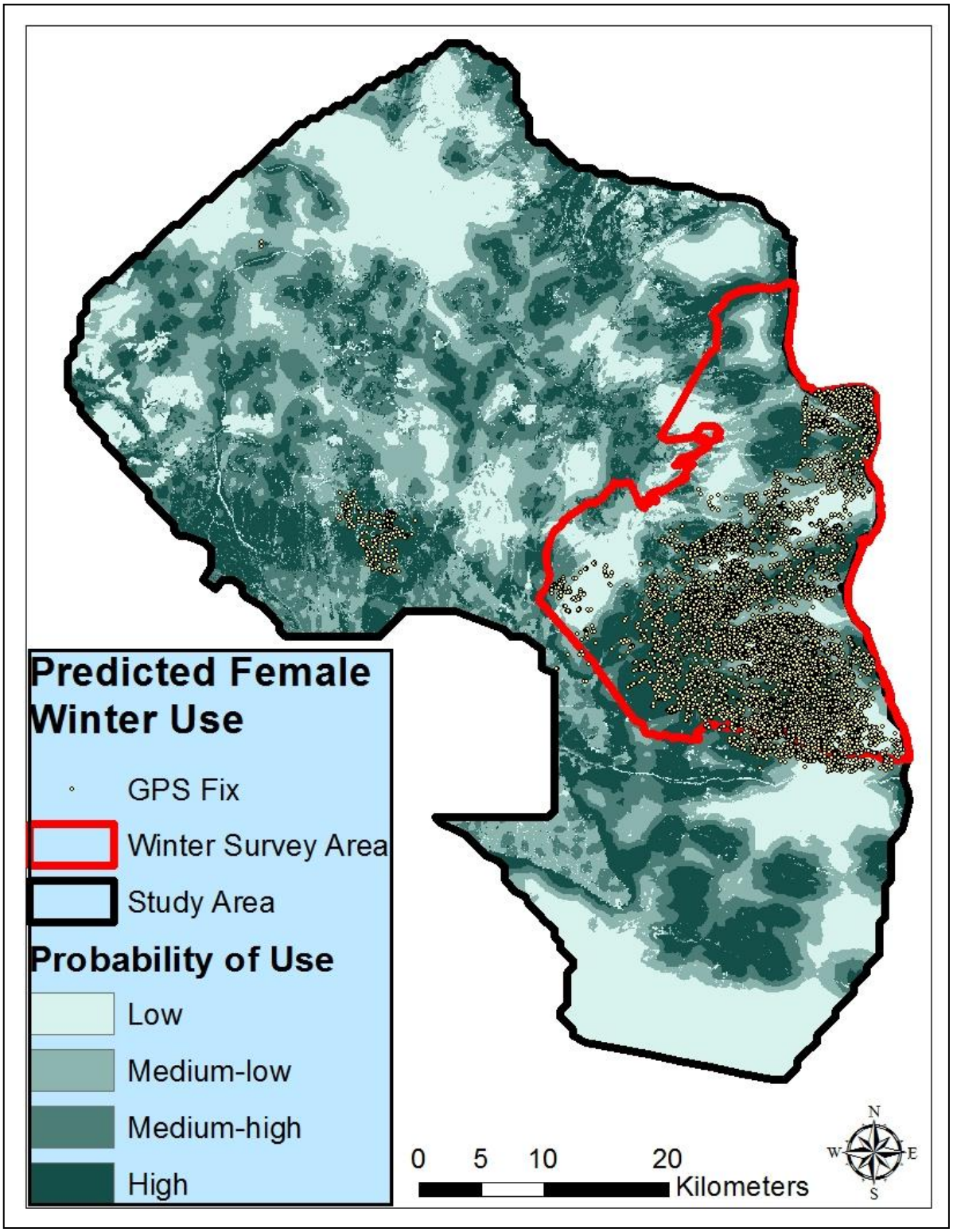

Figure 6 Predictive map showing areas of high and low use across the Colockum herds core range for adult females during the winter season.

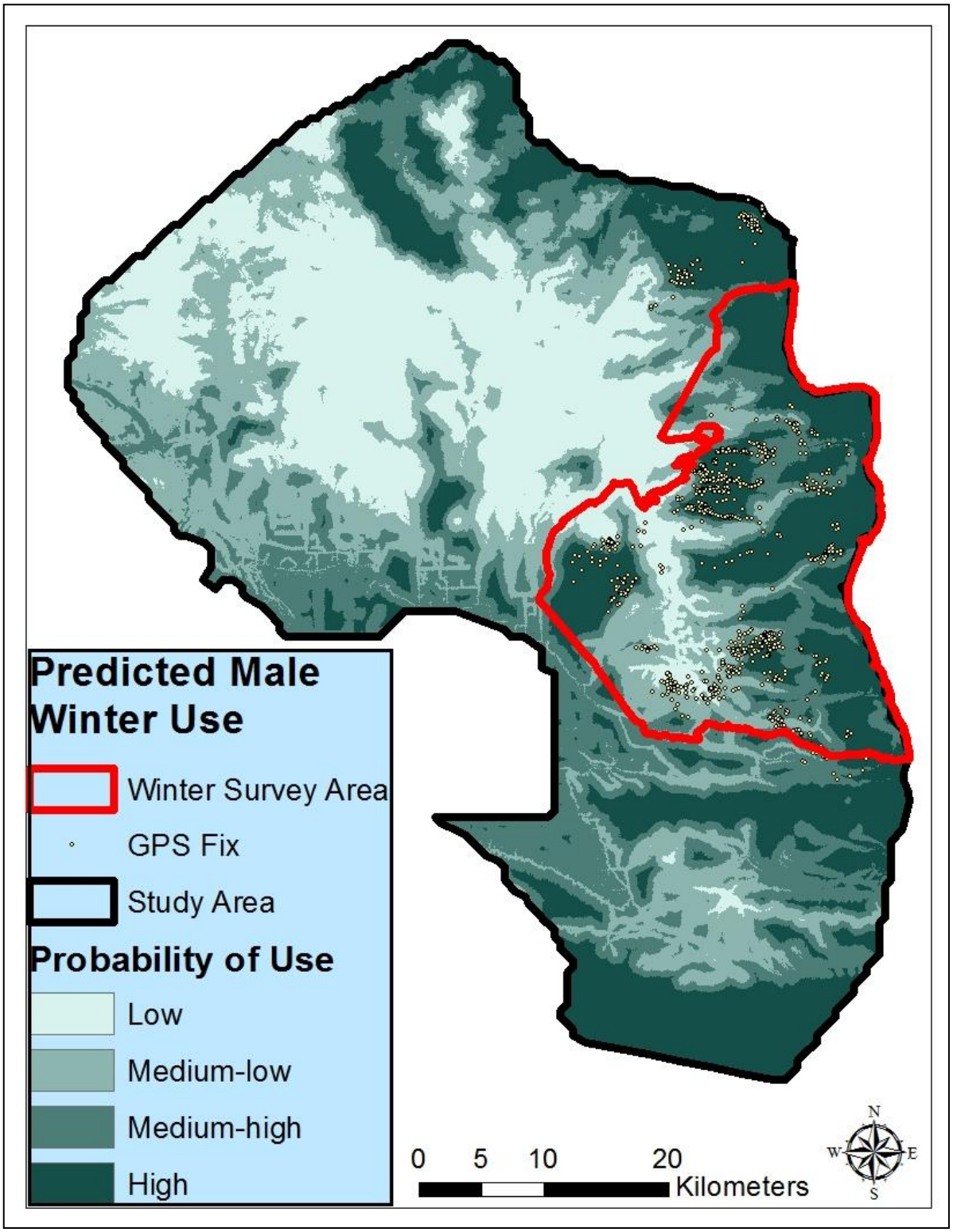

Figure 7 Predictive map showing areas of high and low use across the Colockum herds core range for adult males during the winter season.

Discussion

Habitat segregation hypotheses cite dimorphism between males and females as a key cause for segregation (Ruckstuhl 2007). It is hypothesized that origins of sexual dimorphism arose from monogamous monomorphic ungulates. These species originally occupied closed habitats and then moved into grasslands where polygynous mating systems arose, which in turn gave rise to dimorphism. This was possibly caused by aggregation in relation to clumped food sources in open areas. Ungulates that remained in closed habitats or maintained monogamous mating habits remained monomorphic (Jarman 1974, Pérez-Barbería et al. 2002). Reproductive strategies are also commonly cited to explain why the sexes segregate outside of the mating season. In polygynous mating systems males compete intensely for breeding rights with females. Elk antler size and form reflect fitness and affect fighting success (Clutton-Brock et al. 1980). Cervids that form large breeding groups have large antlers for their body size in comparison to those that form smaller groups (Clutton-Brock et al. 1980). Trivers and Willard (1973) suggested that mechanisms may exist that allow mammalian females to alter birth sex-ratios to reflect their ability to invest in offspring. A female that produces a son ultimately has higher lifetime breeding success than if she produces a daughter because healthy males can reproduce multiple times in one year where females can only reproduce once. Therefore, if a female is in good health it is ideal to produce a son; if she is in poor health, then it is ideal to produce a daughter. A strong son will reproduce more over the course of a lifetime than a strong daughter. A weak son will have a low lifetime breeding success when competing with stronger males and may have no breeding success for multiple seasons. But a weak daughter does not have to compete with females for a chance to breed and can still produce an offspring per season; therefore, a weak daughter is more likely to have a higher lifetime breeding success than a weak son. Forage is of

high importance to females (birth sex ratio) and males (antler size) for increasing their fitness. The difference in strategies for increasing fitness between males and females along with dimorphism has given rise to sexual segregation. Through my study I found evidence that lends some support to several habitat segregation hypotheses.

Road avoidance by elk for both sexes has been well documented (Sawyer et al. 2007, McCorquodale 2003, Unsworth et al. 1998, Montgomery et al.2013). Yet, both males and females used areas closer to roads in summer than winter though both selected for areas near roads, according to my GLM results (Table 1). I believe this is attributed to the higher density of roads on the summer range making it difficult for elk to select for areas away from roads. Areas devoid of roads in the summer range may also lack suitable habitat or nutritional vegetation. Roads are commonly built near streams in the study area where high quality vegetation is common. The summer ranges also have more forest cover lending less sight ability from roads. Montgomery (2013) noted that elk do not relate to all roads similarly and traffic levels affect an elk's use of space. Motorized vehicle access closures in the Quilomene and Whiskey Dick Wildlife Areas go into effect each winter in early February to reduce disturbance to elk on the winter range. Elk avoid roads most likely because of disturbance and vulnerability to hunting (Unsworth et al. 1993). Cover can mitigate the disturbance effect to elk from roads (Lyon 1979). Forest cover is an important feature selected by elk on the Colockum summer and winter landscapes and should be considered in forest management. My findings on elk use of habitat relative to distance to roads did not lend support to any of the 3 habitat segregation hypotheses because selection did not differ between the sexes.

I found that during summer, males preferred to spend their time in canyon bottoms indicated by steep slopes (50% grade) and lower elevations while females preferred to spend

more time near ridge tops indicated by gentle to mild slopes (10-20% grade) and higher elevations. During the winter, males and females used steeper slopes with males using slightly steeper slopes than females. A wide variety of factors could be at play for causing elk to choose steeper slopes in Colockum herd. An explanation for the different choice in slope between males and females in summer may lie with livestock interactions. Elk in east-central Idaho were observed moving to steeper areas in locations where livestock were present (Yeo et al. 1993). Range allotments are present in the Colockum wildlife area and Naneum canyon on elk summer ranges at lower elevations so elk may be choosing higher elevations on steeper slopes to avoid cattle. Elk have been known to use steep slopes to avoid predation from wolves (Mao et al. 2005) so the use of steep slopes is possibly a consequence of genetic programming from their evolutionary history. This is doubtful though because females used mild slopes. Females may choose milder slopes during the summer to make movement easier on their offspring. During winter males and females may choose steeper slopes because they also funnel winds that would uncover edible vegetation from snow pack (Severson and Medina 1983). The eastern side of the study area is dominated by open terrain, giving less shelter from the wind. The results for this could possibly lend support for 2 habitat segregation hypotheses. In the summer the competition for mild slopes dominated by female elk could possibly cause males to seek steeper slopes to find suitable forage. In the winter avoidance of predation could be the reason why females move to steeper slopes as they move to more open habitats and leave behind the protection of the forested areas commonly used on the summer range.

The use of aspect varied between sexes. In the summer, males selected for a variety of aspects suggesting aspect was of relatively minor importance in determining selected habitats. Females selected only southwest facing slopes and avoided north facing ones. Pregnant females

have been known to select southern aspects on mild slopes for giving birth to calves possibly because of early plant development and warmer temperatures (Rearden 2005). During winter, males chose south, southwest, and northeast aspects whereas females chose north, northwest, south, and southwest facing aspects. The use of southern aspects in winter is intuitive because solar radiation melts snow, exposing forage (Dalke et al. 1965, Severson and Medina 1983). I expected elk to select north aspects during summer because of cooler temperatures and succulent vegetation (Skovlin et al. 2002). Using GPS fixes for males and females from all times of day (i.e., day and night) could explain why I saw little selection by males for aspect during the summer. Eight designations may have been too fine-scaled for measuring elk aspect selection. It could also be that my definition of summer was too broad. The drying out of vegetation that takes place from May to September may cause elk to shift aspect preferences through the summer.

Elevation ranges for males and females were not significantly different until winter. In the summer both preferred high elevations with females choosing slightly higher locations than males; male GPS locations tended to cluster near valley bottoms whereas females stayed closer to ridge tops on gentler slopes (Table 1). High elevations should be associated with cooler temperatures for elk and montane forest cover (hiding elk from the view of roads). In winter, males selected relatively higher elevations on winter range but not as high as on summer range. Males were able to avoid high snow pack, but still have access to edge habitat in more forested areas. This was apparent in the predictive map (Figure 7) I created, where forest cover was predicted to be used more heavily by males than females. Elevation was not a useful predictor of winter habitat selection for females, perhaps because females use a large portion of the winter range and a wide range of elevations.

Males and females consistently avoided human use and recently disturbed areas. Summer habitat selection models showed that males and females selected similar habitat types in forested and semi desert land cover types, with females also selecting shrub land, whereas males showed no selection. In winter, males selected semi desert followed by shrub land and forest. Females selected heavily for shrub land followed closely by semi desert; forest cover was selected, but less so. I believe that forest cover was relatively more important to males than to females in winter; perhaps selection by males was affected by energy expenditures during the rut. This loss of energy stores may leave them vulnerable to predators. Profitt et al. (2012) found that elk tended to aggregate in larger groups when using grasslands similar to the Colockum semi desert cover types, than when using forested areas in winter. If males did have lower body condition after the rut that would leave them vulnerable to predation, and because larger groups are more easily detectable it would make sense for them to select forest cover and avoid being in large easily detectable groups. Over the course of summer and winter, females consistently selected shrub lands more than males who selected semi desert (Table 1). Shrub lands in the Colockum contain sage brush which has been shown to be effective in hiding elk calves (Johnson 1951). These findings match expectations for the predation risk hypothesis given females used more shrub land habitat whereas males used more open semi desert habitats in summer.

My findings on elk selection of water matched expectations that in winter and summer males and females would select for areas near water. NDVI consistently showed riparian areas as having higher vegetation quality than areas far from water. Given increasing summer temperatures and senescence of vegetation, areas around creeks and streams should contain higher quality vegetation. Nelson and Burnell (1975) found that elk generally prefer habitats <800m from water in central Washington. Both males and females in my study selected for

habitat within this distance during summer and winter. This finding would best support the forage selection hypothesis as water sources provide high abundance and quality of vegetation.

Plant productivity in spring, indexed using NDVI has been shown to strongly correlate with winter body mass in roe deer (*Capreolus capreolus*) fawns (Pettorelli 2006). NDVI results showed that males selected vegetation with higher photosynthetic activity than females during summer. This is congruent with the predation risk hypothesis in which males accept risk to access better foraging areas, whereas females prioritize security of their offspring (Main et al. 1996). Males may risk using high quality forage in open habitats, but females may not have been as willing to do so. This does not rule out the forage selection hypothesis, because females likely were able to find high quality forage under the forest canopy around moist areas and in riparian zones. It is also possible that given the size of sampling circles (500-m diameter) I missed small areas of high quality vegetation that females did use, but simply were not detected by my analysis. In winter, neither sex selected for NDVI values. This was most likely because understory vegetation was dormant and it was difficult to obtain satellite images with no snow cover. NDVI is difficult to use during the winter for this reason as it is nearly impossible to obtain snow and cloud free images at a consistent date.

Males and Females showed distinctly different selection patterns during the summer and winter. Evidence supporting all 3 habitat segregation hypotheses was present in one or multiple variables in summer or winter. The scramble competition hypothesis was the most challenging to find direct evidence for given the temporal separation between male and female elk studies my data came from. However, I did find evidence that males and females selected for different slopes in winter and summer. Aspect use also differed between sexes in summer and winter; males selected for moderate elevations, whereas females did not select relative to elevation. This

suggested that males and females selected distinct habitats and likely were not within a social distance of each other. The cause for this separation could be competitive exclusion from foraging sites, but that is unlikely given a male's digestive efficiency and range (Ruckstuhl 2007, du Toit 2005). I do not have strong evidence regarding the scramble competition hypothesis.

There was some evidence for the predation risk hypothesis. Males selected for higher vegetation quality than females; females may not have selected for these foraging settings because of greater risk to their calves. Females selected for shrub land cover more than males did; this cover type is known to have abundant sage brush cover suitable for hiding young calves (Johnson 1951). On winter range, females occupied more open habitats than in summer and used steeper slopes that can reduce predation risk (Mao et al. 2005). I conclude it is likely that the predation risk hypothesis plays some role in habitat selection.

There is some evidence in my study supporting the forage selection hypothesis. During summer, females selected for southern aspects, which would green up in early summer. This would be advantageous for nursing females needing to meet lactation requirements. Also females selected for areas near water, which can be associated with quality calving habitat (Bian and West 1997) and enhanced forage quality throughout the summer, despite dry conditions.

To summarize, there are likely multiple factors driving habitat segregation in the Colockum and other elk herds. My indirect evidence best supports the predation risk and forage selection hypotheses, with evidence neither supporting nor refuting the scramble competition hypothesis.

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CHAPTER V

COMPREHENSIVE LITERATURE CITED

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